

ORGANIZATION AND FUNCTION OF CTENOPHORE COLLOBLASTS: AN ULTRASTRUCTURAL STUDY

JEAN-MARIE FRANC

*Histologie et Biologie Tissulaire, Université Claude Bernard, 43,
boulevard du 11 Novembre, 69621 Villeurbanne, France*

The members of the phylum Ctenophora differ from those in the phylum Cnidaria in well defined characteristics, such as the occurrence of swimming comb rows, the presence of an ectomesoderm and the possession of special adhesive cells termed colloblasts. These colloblasts are typically situated on the two tentacles of the Ctenophora, the only known exception being *Euchlora rubra*, in which the colloblasts are replaced by nematocysts (Tregouboff and Rose, 1957).

Early light microscope studies of colloblast structure (Komai, 1922, cited by Hyman, 1940; Weill, 1935a) were complemented by an electron microscope study performed by Hovasse and De Puytorac (1962). For these latter, the colloblast is a single epithelial cell, the apical pole of which (collosphere or colloblast head) is swollen by numerous eosinophilic granules. Each granule is at the end of a dense fibril which arises from a unique star-shaped structure named the "spheroidal body." This, situated in contact with the nucleus, was interpreted as a nuclear extrusion rather than as a centrosome, because the nuclear membrane was apparently absent at their point of contact. The nucleus of the colloblast stretches towards the basal pole of the cell and corresponds to the axial filament described with the light microscope. A second filament, interpreted as the "spiral filament" (helical thread) originates from the spheroidal body, reaches the cell surface, encircles the cell in two or three whorls and runs towards the fibrous axis of the tentacle. This helical thread was described as a non-fibrous tube, surrounded by the plasma membrane expanded into six to ten longitudinal anastomosing cristae (membrane folds). Some refractive vesicles ("brilliant granules") are also situated at the external surface of the colloblast head. A covering cell forms a cap above several colloblast heads and was interpreted as being responsible for transporting the colloblasts along the tentacle.

More recently, Bargmann, Jacob and Rast (1972) published a detailed ultrastructural study of the tentacle of a ctenophore. They observed the features of the colloblast cell described above, as well as new structures such as the bottle brush root ending of an anchoring apparatus and the existence of "procolloblasts" (precursor cells) arising from cells of the covering layer of the tentacle. A new interpretation of the origin of the outer refractive vesicles of the colloblast head was given; they could result from a very fast extrusion of the intracytoplasmic eosinophilic granules. However, their study also included some unusual observations, such as the absence of a nuclear membrane over great parts of the surface of the nucleus. In addition, the structure similar to the "spiral filament" of Hovasse and De Puytorac (1962) was considered to be a straight stalk. As the membrane folds surrounding this stalk had a slightly spiralized disposition,

Bargmann *et al.* (1972) suggested it was these structures that had given rise to the erroneous description of a helical thread by previous authors.

The present study of four species of ctenophores was thus undertaken with a view to elucidating the structure of the colloblast in general and to resolve the above mentioned conflicting observations in particular. Also, new evidence is presented concerning the innervation of the colloblasts and the mechanisms of colloblast activation and adhesion.

MATERIALS AND METHODS

The study was performed on four species of the phylum Ctenophora (*Pleurobrachia rhodopis*, *Eucharis multicornis*, *Cestus veneris* and *Lampetia pancerina*) collected from the bay at Villefranche-sur-Mer (France).

For transmission electron microscopy (TEM), tentillae, tentacles and tentacle bases were fixed with 3% glutaraldehyde and 1% osmium tetroxide, in a 0.1 M sodium cacodylate buffer (pH 7.8). All media were adjusted to the osmolarity of sea water. After embedding in Epon, thin sections were stained with uranyl acetate and lead citrate (Reynolds, 1963) and examined in Philips EM300 and Hitachi HU12A electron microscopes.

Specimens of *Pleurobrachia* were fed *Artemia* nauplius larvae (Crustacea, Branchiopoda) and tentacles and tentillae which had captured larvae were cut off, fixed and embedded as above.

Two preparations were used for scanning electron microscopy (SEM): first, isolated tentacles of *Pleurobrachia* and body fragments with their tentacular sheets, and secondly, tentacles of *Eucharis* which had "captured" glass coverslips. After double fixation, the specimens were critical-point dried using acetone-carbon dioxide, then sputter coated with gold and observed in a Cambridge S600 scanning electron microscope.

RESULTS

The tentaculate Ctenophora bear two very long contractile tentacles, situated on either side of the sagittal plane, which is determined by the pharynx of the animal. Many shorter and thinner contractile filaments occur along each tentacle and, in *Eucharis* and *Cestus*, around the lips. These constitute the tentillae (Fig. 1). Tentacles and tentillae have the same organization: an axis of muscle cells embedded in a dense fibrillar mesoglea (Franc, Franc and Garrone, 1976) within which lie the elements of the tentacular nerve, and a peripheral cortex consisting of epithelial cells, mucous cells, sensory cells and colloblasts. The colloblasts are more numerous on tentillae than on tentacles. The sensory cells each possess a non-motile cilium and sometimes also show sensory peg structures as described by Hernandez-Nicaise (1974b). They are grouped into clusters and are always associated with mucous cells. These sensory clusters constitute an extensive surveillance system over the surface of the widespread tentacular apparatus (Fig. 2).

Colloblast organization

Seen with SEM (Fig. 3) or TEM (Fig. 4), the mature colloblast is a single pear-shaped cell, anchored to the tentacular mesoglea by its slender basal end. The size of these cells varies with the species studied: the smallest are found in *Pleurobrachia* where they are $10\ \mu$ in length and a maximum of $4\ \mu$ wide, whereas in *Eucharis* the colloblast may reach a length of $25\ \mu$ and a width of 8 to $10\ \mu$. However, the length also varies considerably depending on their degree of extension at fixation.

The colloblast always contains a nucleus which is elongated and whose form follows that of the pear-shaped cell (Fig. 4). It is surrounded by a typical nuclear membrane and contains evenly dispersed, thin, granular chromatin. No nucleolar structure was detected in the mature colloblast. Some mitochondria, occasional rough endoplasmic reticulum cisternae and few vesicles and microtubules are located in the cytoplasm.

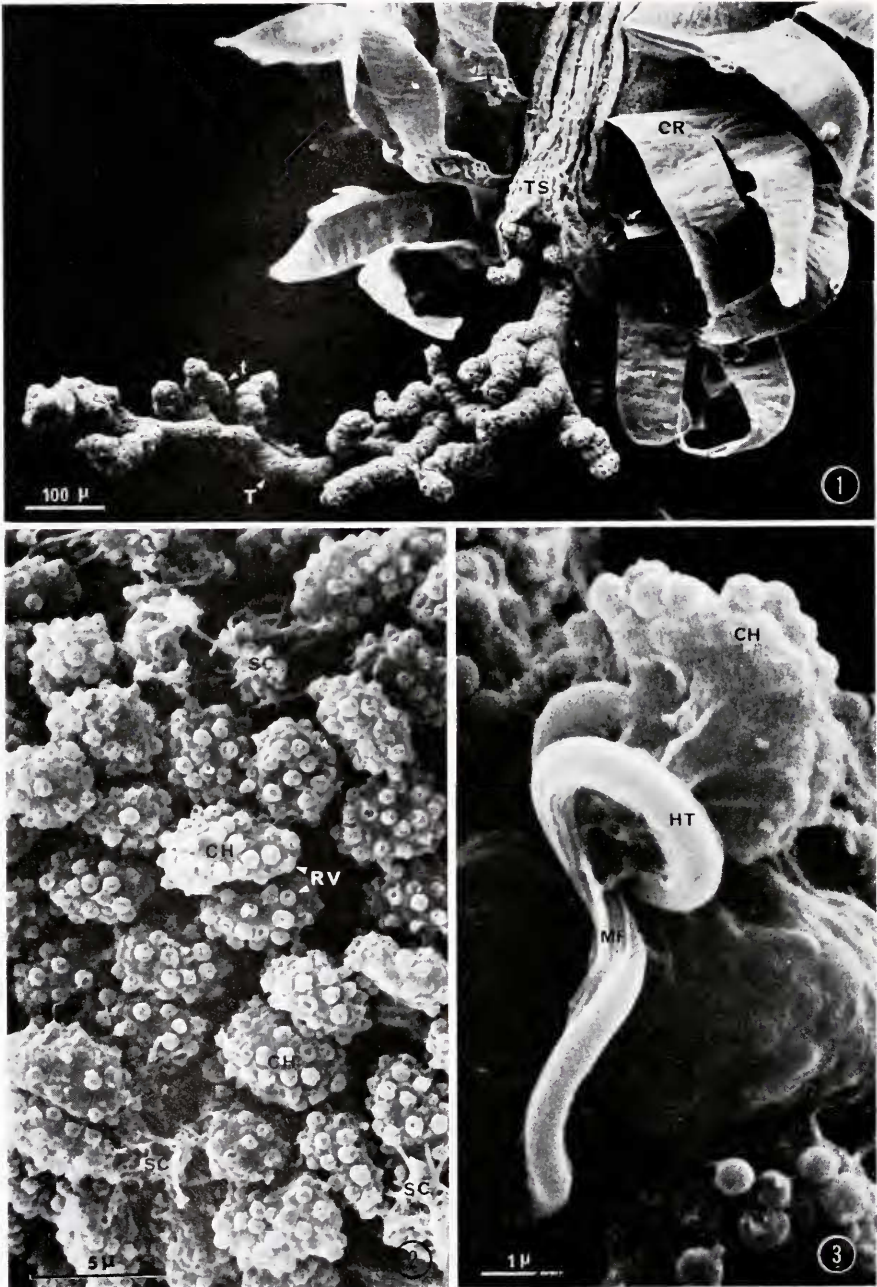
The expanded end of the colloblast contains numerous peripheral granules (Fig. 4). These correspond to the "eosinophilic granules" of light microscopy. They are membrane bound spherical vesicles about $0.8\ \mu$ in diameter, with finely granular contents and may show dense, secondary concentric or radial formations, in the mature state (Fig. 5). Above these granules, the colloblast plasma membrane bears a particularly well developed cell-coat with a hexagonal substructure (Fig. 6).

The colloblast head generally bears several indented vesicles (Figs. 2, 4, 5). Irregular in outline and containing variable amounts of electron dense material, these vesicles lie external to the colloblast membrane in the hollows between the eosinophilic granules. Neither connection of the colloblast membranes with those of the external vesicles, nor evidence of extrusion of granules from the colloblast has been observed. By virtue of their position, these vesicles can be identified with the "refractive vesicles" of light microscopy.

Apart from the eosinophilic granules and the refractive vesicles, the principal feature of the colloblast cell is the presence of a helical thread. This intracellular structure extends from the base to the apex of the cell and is generally in the form of a right hand helix, but is occasionally left-handed. Although the helical thread is loosely coiled for the first two turns, it later tightens before heading towards the center of the colloblast head. The diameter (0.25 – $1.25\ \mu$), length and number of turns of the helical thread vary with the origin of the colloblast. In *Lampetia* and in *Cestus* there are but one or two turns (Figs. 7, 8), whereas in *Eucharis* the thread is tightly coiled and there are six to seven turns of the helix (Fig. 9).

Where the helical thread follows the cell surface, it lifts the plasma membrane but remains connected to the cell body by a thin strip of cytoplasm (Fig. 10, arrows). Parallel to this strip, the membrane expands in five to eight folds which longitudinally follow the inner surface of the helical thread as far as its penetration into the colloblast head. Here, the folds of the membrane gradually diminish and then disappear. Along its invagination into the cell, the plasma membrane forms a double sheath around the end of the helical thread.

In section, the thread is heterogeneous. A cortex is well differentiated in *Pleurobrachia* and less easily seen in *Cestus* and *Eucharis*. The core can be



FIGURES 1-3. SEM of the tentacle of *Pleurobracmia rhodops*.

FIGURE 1. View of a tentacle (T) with tentillae (t) emerging out of the tentacle sheath (TS). Comb rows (CR) are visible on either side of the sheath.

FIGURE 2. Surface view of a tentilla. The heads of the colloblasts (CH) bear outer

very electron dense (*Lampetia*, *Pleurobrachia*) or can present a lighter, finely granular structure (*Cestus*, *Eucharis*, *Pleurobrachia*). Within this core, six to nine peripheral simple longitudinal microtubules can be observed in the early stages of colloblast formation (Fig. 11).

The distal end of the helical thread terminates at the upper part of the nucleus and is differentiated into a structure commonly called the "spheroidal body". This consists of very dense material, in continuity with the cortex of the helical thread, and covering its distal end. This spheroidal body is set more or less in a hollow in the upper part of the nucleus which can even surround the distal end of the helical thread. However, the nucleus is invariably separated from the spheroidal body by a continuous nuclear membrane (Fig. 12). From the spheroidal body radiate fibrillar extensions, named radii, each of which terminates on one of the peripheral eosinophilic granule (Figs. 4, 7, 9, 12). At the point of contact, this radius is enlarged to produce a small attachment patch which bears a tuft of fine fibrils (Fig. 5). These are attached to a thickening on the outer surface of the granule membrane, on the inner side of which is a localized increase in density of the vesicle content. It is from here that the dense secondary formations in the mature eosinophilic granule arise.

At the opposite end of the helical thread is an electron dense, cone-shaped root structure. In *Lampetia*, it has a finely fibrillar organization, more or less packed in bundles with an axial periodicity of about 850 Å (Fig. 13). The surface of the root is bristled with numerous, thick filaments, giving it the appearance of a bottle brush (Figs. 13, 14). This root extends the colloblast plasma membrane into the intermuscular mesoglea of the tentilla. Here, the colloblast foot is enclosed in a thin jacket of extracellular material to which are attached massive fibers, specific to this mesoglea.

A synaptic junction always occurs in an expansion of the colloblast cell membrane, which is situated either at the basal region of the helical thread or just above the root structure (Fig. 14). The synaptic cleft is 100 to 125 Å wide. In the neurite ending, small electron-lucent vesicles 700 to 1000 Å in diameter line the presynaptic membrane. They are associated with a cisternum of the endoplasmic reticulum and a mitochondrion. However, often these latter two organelles are not visible; in which case, the synaptic junction is characterized only by the presence of the lining vesicles and the parallel array of the two plasma membranes. This synapse is always polarized in the same direction, towards the colloblast. Occasionally, the same neurite appeared to form synapses with several colloblasts or even with mucous cells and colloblasts.

Specialized epithelial cells constitute a continuous cover on the tentacle. Upon the tentilla, and possibly at the tentacular ends, these covering cells become irregular. They occupy the free spaces between the sensory elements, the mucous cells and the heads of mature colloblasts to which they are linked by a *zonula adherens*.

refractive vesicles (RV), some of which are depressed. Three sensory complexes (SC) are seen breaking through the surface of the tentilla.

FIGURE 3. Higher magnification of a colloblast partially removed from the tentacle. The membrane folds (MF) running along the helical thread (HT) are visible due to partial disruption of the cell body. CH shows colloblast head.

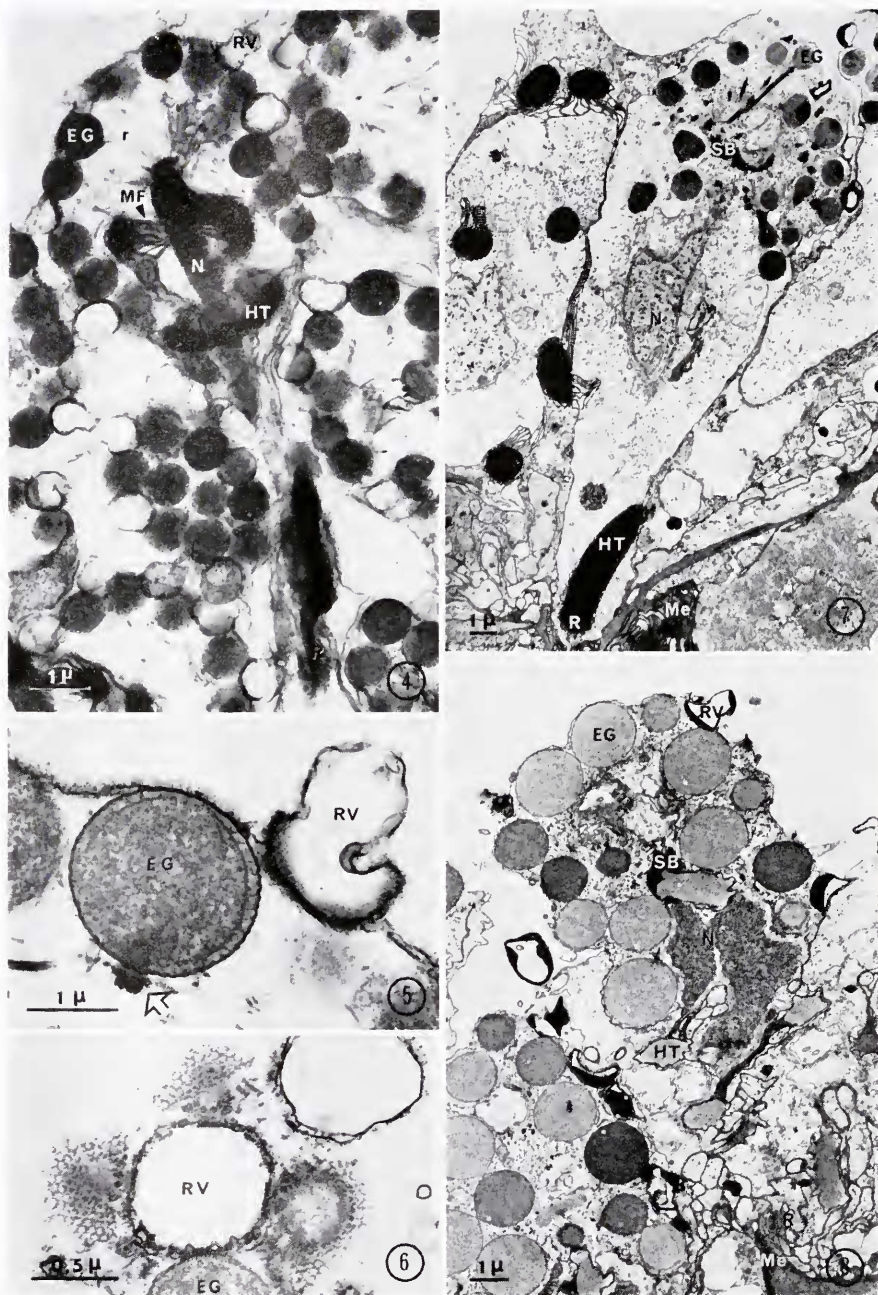


FIGURE 4. TEM of a thick section (0.5μ) of a *Pleurobrachia* colloblast. EG shows inner eosinophilic granule; HT, helical thread; MF, membrane folds; N, nucleus; R, root; r, radius; RV, outer refractive vesicle.

Capture phenomenon

In their natural state, or removed from the animal, tentacles and tentillae consistently stick to a glass rod or an *Artemia* larva put in contact with them. This reaction will occur repeatedly with the same tentacle, but is eventually abolished by too frequent touching with the glass rod and does not occur if the animal has its pharynx full of prey.

Comparing cross sections of tentillae originating from a resting *Pleurobrachia* and from a *Pleurobrachia* activated by a captured *Artemia* larvae, two main differences appear. The first is the presence of a clear area between the musculo-mesogleal axis of the activated tentilla and its external sheet of colloblast heads. This area consists of the cytoplasmic extensions and loose helical threads of the colloblasts embedded in a finely granular mesoglea from which the massive fibers are completely absent. The second difference is the position of the sensory cells relative to the colloblast heads. In the resting tentillae, the colloblast heads are situated at the level of the sensory cells and, consequently, the sensory cilia protrude from the surface of the tentilla. In the activated tentillae, however, the colloblast heads extend beyond the sensory cells, which remain at their original level.

In SEM examination of tentacles attached to glass coverslips, the sticking phenomenon appears localized. At the contact points, the gluing substance covers the surface of the "prey" in those places where the colloblast heads lie. These may or may not be connected by threads to their tentilla. Often the helical thread is not visible and the wall of the foot seems uniform because of the presence of the covering cells. In other cases, the helical thread lies unfolded along the cell body, but complete extension of the helical thread is rare. Colloblasts not in contact with the "prey" appear unmodified.

In TEM examinations of tentillae which have captured an *Artemia* larva (Fig. 15), the crustacean cuticle bears a coarse, granular product in which are seen empty, membrane-bounded cavities with irregular outlines. Also present may be the remains of colloblast heads partly surrounded by their cytoplasmic membranes and containing some intact eosinophilic granules, as well as the anterior end of the helical thread and the more or less extended radii. The adhesive substance contains electron dense filaments, some of which converge onto the same point. Here, a structure similar to the small attachment patch of the eosinophilic granules is recognizable (Fig. 15, arrow).

Straightened helical threads are observed only on such preparations. The diameter and the inner structure of each thread remain identical to that of the

FIGURE 5. Detail of an eosinophilic granule (EG) with its secondary dense formations and the attachment patch (arrow). RV shows refractive vesicle.

FIGURE 6. Tangential section of the cell-coat of the colloblast head. EG shows eosinophilic granule; RV, refractive vesicle.

FIGURE 7. Longitudinal section of a colloblast of a *Lampetia* tentacle. EG shows eosinophilic granule; HT, helical thread; Me, mesoglea; N, nucleus; R, root; SB, spheroidal body.

FIGURE 8. Colloblast from a buccal tentilla of *Cestus*. Legends as in Figure 7.

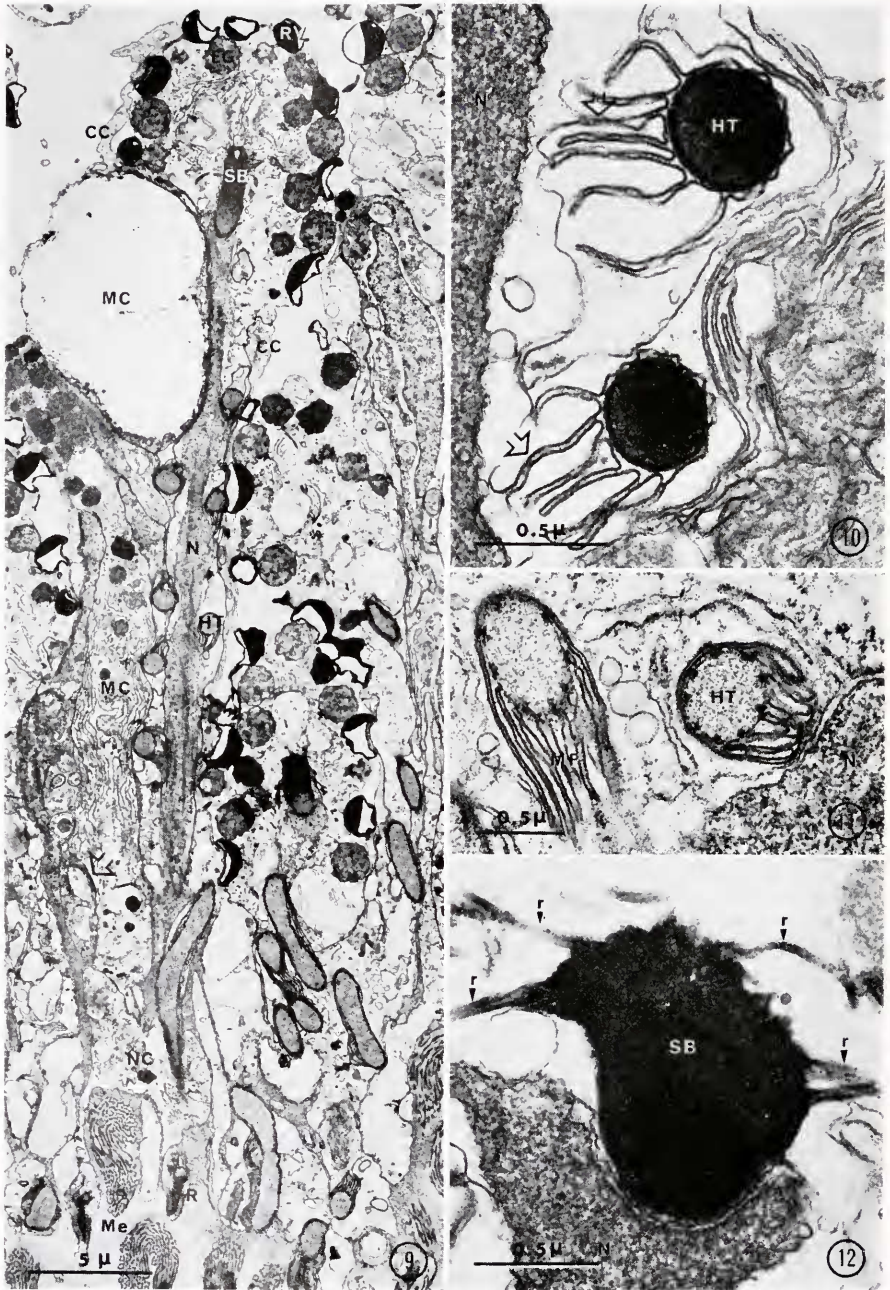


FIGURE 9. Longitudinal section of a colloblast of an *Eucharis* tentilla; note the nerve ending (arrow) connecting a mucous cell (MC). CC shows covering cell; EG, eosinophilic granule; HT, helical thread; Me, mesoglea; N, nucleus; NC, nervous cell; R, root; RV, refractive vesicle; SB, spheroidal body.

supposed resting colloblast, but cell shape and the arrangement of the membrane folds change. A marked reduction of the cell body diameter is seen corresponding to its increased length. In cross sections of the basal region of such a cell, the helical thread and sometimes the nucleus are visible, closely enveloped in the plasma membrane. The membrane folds are still present, but now are arranged in a loose helix around the straightened helical thread.

DISCUSSION

The present study has included representatives of each order of the Tentaculata Ctenophora, except for the Platyctenea, which live mainly in warm waters (Hyman, 1940). Colloblasts from all the animals studied were found to be similar in structure, differing only in details such as their overall size or the length of the helical thread. This applies to both colloblasts borne on tentacular tentillae and those of buccal tentillae. The present observations confirm the unicellular nature of the colloblast throughout the ctenophores. Its generalized structure is given in Figure 16.

The scarcity of cytoplasmic organelles and the absence of a nucleolus indicate the low level of synthesis in the mature cell. However, no sign of degeneration was observed in either the resting or the active colloblast. The incomplete nature of the nuclear membrane described by Bargmann *et al.* (1972) may be a fixation artifact, as optimal fixation is often difficult in animals such as ctenophores which have a high water content.

The ultrastructural examination of captured *Artemia* larva shows that the eosinophilic granules are responsible for the gluing action of the colloblast. The capture phenomenon involves the disruption of the colloblast. Many of the released eosinophilic granules burst, liberating their glue, which traps the prey and attaches it to the fibrous radii of the spheroidal body. Consequently, *the capture mechanism of the colloblast is self-destructive*. The outer refractive vesicles seem to play no part in the capture mechanism. This is in agreement with their weak adhesive properties (Weill, 1935b) and their irregular arrangement or absence from the surface of the colloblast head.

Bargmann *et al.* (1972) considered that the refractive vesicles are extruded eosinophilic granules whose contents have been rapidly transformed. Present observations do not support this interpretation. On the contrary, in an initial study on the histogenesis of the tentacular cortex (unpublished results), it was found that the refractive vesicles are the remains of an accessory cell which disappears during tissue differentiation.

FIGURE 10. Two transverse sections of the helical thread (HT) from a *resting* colloblast of *Pleurobrachia*; the cell membrane exhibits five to six folds as it wraps around the thread. Arrows show the thin strip of cytoplasm connecting this structure to the cell body; N, nucleus.

FIGURE 11. Two cross sections of a helical thread of an *Eucharis* immature colloblast. Note the nine peripheral microtubules. MF shows membrane folds.

FIGURE 12. Expanded distal end of the helical thread constituting the spheroidal body (SB) with fibrous radii (r) radiating from it; note the continuity of the membranes and space around the nucleus (N) and the close association between the spheroidal body and the outer nuclear envelope (*Pleurobrachia rhodopis*).

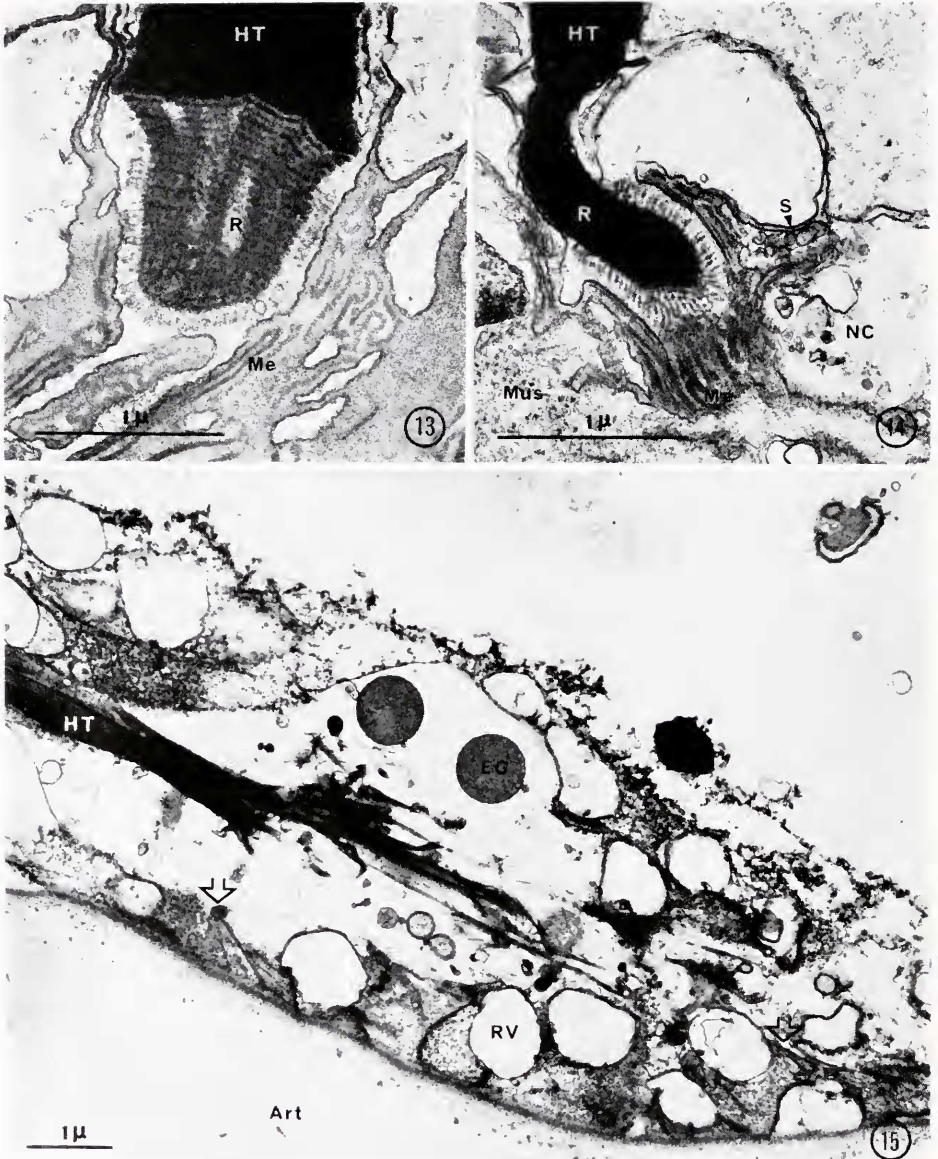


FIGURE 13. Longitudinal section of the colloblast root (R) in *Lampetia*. Note its periodic structure reminiscent of a ciliary rootlet. HT shows helical thread; Me, mesoglea.

FIGURE 14. Longitudinal section of the root (R) of a *Pleurobrachia* colloblast, embedded in the mesoglea (Me) between muscle cells (Mus). A polarized synaptic ending (S) makes contact with an expansion of the colloblast cell membrane. HT shows helical thread; NC, nervous cell.

FIGURE 15. Head of a *Pleurobrachia* colloblast adhering to the cuticle of an *Artemia* larva (Art). The burst eosinophilic granules have released a gluing substance in which attachment patches with the secondary dense formations (arrows) are still recognizable; some eosinophilic granules (EG) are still intact. HT shows helical thread; RV, refractive vesicle.

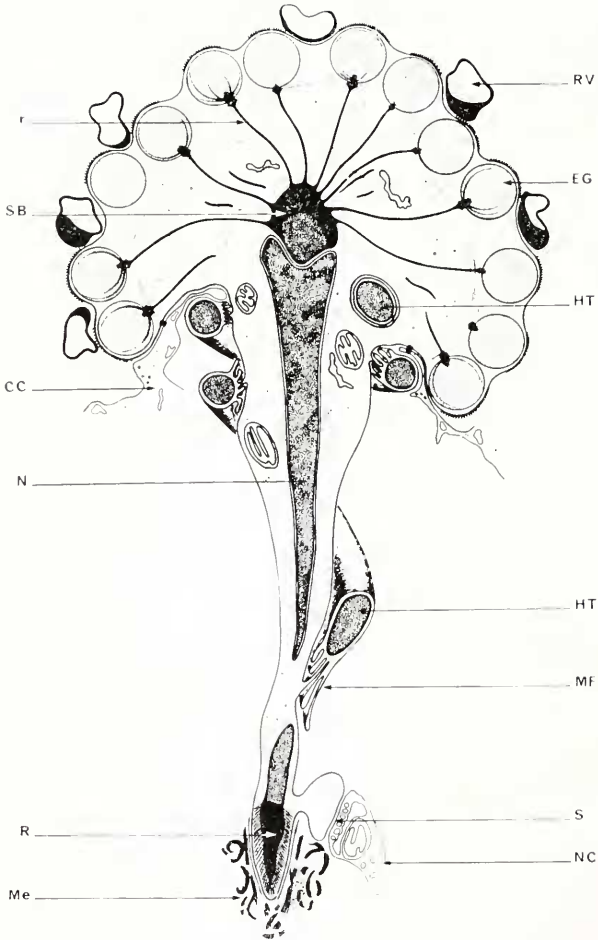


FIGURE 16. Schematic drawing of a resting colloblast as seen with the electron microscope; to emphasize its helical form, the thread is partly represented in shadowed perspective. CC represents covering cell; EG, eosinophilic granule; HT, helical thread; Me, mesoglea; MF, membrane folds; N, nucleus; NC, nervous cell; R, root; r, radius; RV, refractive vesicle; S, synapse; and SB, spheroidal body.

The helical form of the thread of the resting colloblast was demonstrated both by SEM and by TEM observations of thick sections of tentillae. This confirms the early light microscope studies of Komai (1922, cited by Hyman, 1940) and Weill (1935a), and the first electron microscopy description by Hovasse and De Puytorac (1962). However, Bargmann *et al.* (1972) considered that the "spiral filament" seen by light microscopy was in fact the helically arranged membrane folds surrounding a straight tube. This discrepancy can be explained as follows. In a *resting* colloblast, the membrane folds follow the helical thread along the generatrix line facing the longitudinal axis of the cell (Fig. 17a). But, in an *extended* colloblast, it is the membrane folds that form a loose helix around the straightened thread (Fig. 17b). This arrangement results

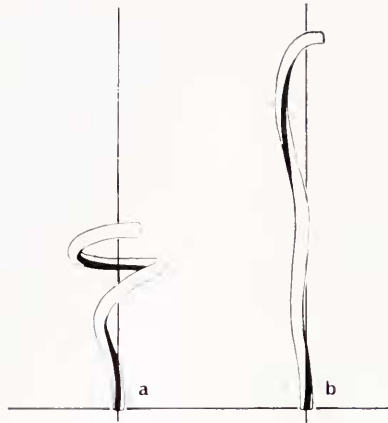


FIGURE 17. Relative positions of the membrane folds (black) on the thread (clear) in its helical (a) and extended (b) conditions.

from the relative movement between the membrane folds and the helical thread *without rotary motion of their ends* during extension of the cell. This is assured by the anchoring of the thread in the tentillar mesoglea and the *zonula adherens* junction binding the colloblast head to the surrounding covering epithelial cells. It is probably on colloblasts in this latter condition that Bargmann *et al.* (1972) based their interpretation.

No modification in diameter or content of the thread was observed between its resting or extended state. The various aspects of the helical thread matrix are observed on different tentillae of the same tentacle and may thus be related to the maturity of the cell, the clearer matrix corresponding to the most differentiated state.

The presence of microtubules at the periphery of the helical thread, the close association of its distal end with the nucleus and the ciliary root-like structure observed in *Lampetia* could suggest a ciliary origin for the helical thread. However there are significant differences between this thread and the well-known flagellar structures (Afzelius, 1969). For example, no basal body structure was ever seen in a mature colloblast, either at the root end or at the spheroidal body. The peripheral microtubules of the thread are not in a doublet or a triplet arrangement and no central microtubules are present. If not indicative of a ciliary origin, the peripheral microtubules may have a skeletal function (Pochon-Masson, 1967).

In spite of their close resemblance at the light microscope level, the helical thread differs from the protozoan peritrich ciliate stalk (Amos, 1972; Favard and Carasso, 1965; Huang and Pitelka, 1973) by the absence of microfilaments. The paucity of microtubules means that an analogy between the colloblast helical thread and the axostyle of certain protozoan flagellates (Grimstone and Cleveland, 1965) cannot be considered seriously. A similarity can only be established between the colloblast and prehensile tentacle of certain protozoan suctorians (Batisse, 1965, 1966; Rudzinska, 1965) on the basis of their function (prey capture) and mechanism (gluing).

It is evident that the helical form of the thread assures a resilient attachment of the prey to the tentacle. Curiously, this helical shape is found elsewhere only in the evaginated filaments of the cnidarian nematocysts, which also have a gluing function (Mariscal, 1974). It remains to be established *how* the colloblast contacts its prey. It could occur by contact of the prey with the colloblast or by projection of the colloblast head towards the prey. The differences observed between a resting tentilla and a stimulated one suggest that excitation of one (or a few) sensory cilia could cause the elevation of all the colloblasts borne on a tentilla, but not their destructive projection. From a functional point of view, the retracted position of colloblasts on a resting tentilla would expose the sensory cilia, whereas the elevated colloblasts would more effectively expose the potentially adhesive colloblast heads.

Although a more complete study is needed to answer this question, the discovery of colloblast innervation corroborates the hypothesis of an activation process. This synaptic junction is identical with those previously described in ctenophores (Hernandez-Nicaise, 1968, 1973). The presynaptic organelles which constitute the "presynaptic triad" were consistently found in the nervous compartment of the synapse and indicate that the colloblast acts as an effector. It must be stressed that each colloblast bears a polarized synapse, as do cnidarian nematocytes (Westfall, 1969, 1970). Hernandez-Nicaise (1974a) presented histological evidence that sensory cells are indeed neurons which can connect directly with effector cells, especially in the tentacular epithelium. However, these sensory cells themselves also receive neuro-sensory polarized synapses in which they are the post-synaptic elements (Hernandez-Nicaise, 1974b). Consequently, it is possible that a direct sensory-motor pathway occurs between a sensory cell and a colloblast. If this is so, then a functional homology between the cnidarian nematocyte and the sensory cell-colloblast complex of ctenophores can be considered. To emphasize this, it is of interest to notice the close resemblance between the endocil-stereocilium apparatus of the nematocyte described by Westfall (1970) in a hydro-medusan, and the cilium and peg differentiations of the ctenophore sensory cell (Hernandez-Nicaise, 1974a).

As the capture of prey causes the destruction of colloblasts, each can be used only once. Now colloblasts must therefore be continually formed. This occurs in the lateral thickenings of the tentacle base epidermis (Hyman, 1940). The colloblasts are well differentiated when they arrive on the tentacle. The only modifications found were maturation of the eosinophilic granules, clearing of the dense matrix of the helical thread and integration of the colloblast cell by the nervous system. In particular, the "procolloblasts" described by Bargmann *et al.* (1972) do not exist on the tentacle. On the other hand, the presence of the covering epithelial cells is confirmed. Initially having a protective function at the tentacular level, these cells later assure the continuity of the tentilla epithelium.

Experimentation was performed at the Station Zoologique of Villefranche-sur-Mer, Université Pierre et Marie Curie (Paris) and electron microscopy observations at the Centre de Microscopie Electronique Appliquée à la Biologie et à la Géologie, Université Claude Bernard (Villeurbanne).

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SUMMARY

The fine structure of ctenophore colloblasts was examined using scanning and transmission electron microscopy.

The same structure was found consistently in the three largest orders of the main class of Ctenophora (Tentaculata).

The colloblast is a pear-shaped cell, firmly anchored in the tentacular mesoglea by its tapering base. This highly specialized cell is always nucleated and contains an intracytoplasmic helical thread which divides into numerous fibrous radii at its distal end. Each radius bears at its tip an eosinophilic granule containing a mucoid substance which, when released by contact with the prey, glues it to the tentacle. The outer refractive vesicles, which are interpreted here as the remains of another kind of cell, seem to play no part in the capture phenomenon.

The innervation of the colloblast by a chemical synapse is described and discussed with respect to functional mechanics and phylogeny.

The colloblast appears to be a disposable capture cell and a new scheme of its organization is proposed.

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